

An evolutionary perspective on caching by corvids

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A principal finding in the food-caching literature is that species differences in hoarding propensity are positively correlated with species differences in degree of adaptations to caching behaviour, such as performance on spatial memory tasks and hippocampal volume. However, there are examples that do not fit this pattern. We argue that these examples can be better understood by considering the phylogenetic relatedness between species. We reconstruct the ancestral state for caching behaviour in corvids and assess when transitions in caching behaviour occurred within the corvid phylogeny. Our analysis shows that the common ancestor of all corvids was a moderate cacher. This result suggests that corvids followed a bi-directional evolutionary trajectory in which caching was secondarily lost twice and there were at least two independent transitions from moderate to specialized caching. The independent evolution of specialized cachers in the two groups must, therefore, be a case of convergent evolution. This is exemplified by the fact that specialized cachers show structurally different adaptations serving the same function to intense caching, such as different pouches to transport food. Finally, we argue that convergent evolution may have led to adaptations in memory and hippocampus that serve the same function but differ in design, and that these different adaptations may explain the examples that do not fit the pattern predicted by the adaptive specialization hypothesis.

Keywords: spatial memory; hippocampus; adaptive specialization; food hoarding; phylogeny; corvid

1. INTRODUCTION

A number of bird species cache food for later consumption (Vander Wall 1990). It has been argued that food-caching will only be an evolutionarily stable strategy if the cacher employs a strategy that makes it more likely to recover its own caches as opposed to the caches being recovered by other individuals (Andersson & Krebs 1978; but see Smulders 1998; Vander Wall & Jenkins 2003). One such strategy is to remember the exact location of the caches. Krebs (1990) argued that the increased visuo-spatial demands of remembering the locations of thousands of food caches might have resulted in an enlargement of the hippocampus, an area of the brain that is known to play a role in memory for cache locations (Sherry *et al.* 1989; Smulders & DeVoogd 2000). The adaptive specialization hypothesis, thus predicts that food-cachers should have larger hippocampal volumes, relative to overall brain size, than non-cachers. Comparative analyses across families or sub-families of birds confirm that food-caching species have larger relative hippocampal volumes than non-cachers (Krebs *et al.* 1989; Sherry & Vaccarino 1989; Garamszegi & Eens 2004).

Corvids show variation in caching behaviour, from species that do not cache at all to others that are highly dependent on their caches during periods of food shortage. Concordantly, corvids show variation in adaptations to food caching and recovery behaviour such as pouches for transporting food. The variation in reliance on stored food allows a further test of the adaptive specialization hypothesis, namely that those species that are more reliant on cached food and cache more intensively should have more pronounced adaptations to food caching behaviour than those that cache less intensively. Tests of this

hypothesis that compare performance in spatial memory tasks and hippocampal volume in species that show variation in caching behaviour have led to mixed results, ensuing a debate over the validity of the approach (e.g. Bolhuis & Macphail 2001; Healy *et al.* 2005).

Part of the problem may lie in the fact that most studies that test the adaptive specialization hypothesis implicitly assume that the presence of an adaptation in one species is the derived state and the absence of that adaptation in a related species is the ancestral state. However, when comparing species' adaptations to current selection pressures it is crucial to know the state of that trait in the common ancestor. If the common ancestor showed the trait, then it is the absence of the trait in extant species that signifies an adaptation. Indeed, reverse evolution (loss of derived traits), is much more prevalent than previously assumed (Teotonio & Rose 2001; Wiens 2001; Porter & Crandall 2003), a fact that is known as a result of the development of phylogenetic techniques.

In this paper, we reconstruct the ancestral state of caching in corvids. We then trace the evolutionary transitions of caching behaviour over the phylogeny of corvids and discuss the implications of the reconstruction in relation to adapted traits of food-cachers.

2. MATERIAL AND METHODS

We follow Goodwin (1986) for the species included in the family Corvidae. Information on caching behaviour was obtained from the literature (see table 1). We only included those corvid species for which information about their caching behaviour was available. Only for three corvid species have estimates been made about their caching propensity in natural conditions (Balda *et al.* 1997). Western scrub-jays cache considerably fewer pine seeds (6000) per season than pinyon jays (22 000) or Clark's nutcrackers (33 000).

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Table 1. Caching category and reference for the species used in the analyses.

scientific name	English name	caching category	reference
<i>Cyanocitta cristata</i>	blue jay	3	Darleyhill & Johnson (1981)
<i>Cyanocitta stelleri</i>	Steller's jay	3	Balda & Kamil (2002)
<i>Gymnorhinnus cyanocephalus</i>	pinyon jay	3	Balda & Kamil (1998)
<i>Aphelocoma coerulescens</i>	Florida scrub-jay	2	Woolfenden & Fitzpatrick (1984)
<i>Aphelocoma californica</i>	western scrub-jay	2	Balda & Kamil (1998)
<i>Aphelocoma ultramarina</i>	grey-breasted jay	2	Balda & Kamil (1998)
<i>Cyanocorax caeruleus</i>	azure jay	2	Sick (1993)
<i>Cyanocorax cyanopogon</i>	white-naped jay	2	Sick (1993)
<i>Cyanocorax dickeyi</i>	tufted jay	2	Goodwin (1986)
<i>Calocitta formosa</i>	white throated magpie jay	1	E. Berg, personal communication
<i>Perisoreus canadensis</i>	grey jay	3	Waite & Reeve (1992)
<i>Perisoreus infaustus</i>	Siberian jay	3	V. Pravosudov, personal communication
<i>Garrulus lanceolatus</i>	lanceolated jay	3	Turcek & Kelso (1968)
<i>Garrulus glandarius</i>	Eurasian jay	3	Bossema (1979)
<i>Garrulus lidthi</i>	Lidth's jay	3	Turcek & Kelso (1968)
<i>Nucifraga columbiana</i>	Clark's nutcracker	3	Balda & Kamil (1998)
<i>Nucifraga caryocatactes</i>	spotted Nutcracker	3	Turcek & Kelso (1968)
<i>Cyanopica cyana</i>	azure winged magpie	2	Turcek (1961)
<i>Pica pica</i>	magpie	2	Birkhead (1991)
<i>Pica nuttallii</i>	yellow billed magpie	2	Bent (1964)
<i>Urocissa caerulea</i>	Taiwan magpie	2	Goodwin (1986)
<i>Urocissa flavirostris</i>	gold-billed magpie	2	Goodwin (1986)
<i>Urocissa erythrorhyncha</i>	blue magpie	2	Goodwin (1986)
<i>Cissa chinensis</i>	green Magpie	2	Vernon (1913)
<i>Dendrocitta vagabunda</i>	rufous treepie	2	Goodwin (1986)
<i>Podoces panderi</i>	Pander's ground jay	2	Rustamov (1954)
<i>Pyrrhocorax pyrrhocorax</i>	chough	2	Turner (1959)
<i>Pyrrhocorax graculus</i>	Alpine chough	2	Strahm (1960)
<i>Corvus monedula</i>	jackdaw	1	Henty (1975)
<i>Corvus frugilegus</i>	rook	2	Simmons (1968)
<i>Corvus corone</i>	carriion crow	2	Goodwin (1986)
<i>Corvus splendens</i>	house crow	2	Goodwin (1986)
<i>Corvus macrorhynchos</i>	large-billed crow	2	Goodwin (1986)
<i>Corvus moneduloides</i>	New Caledonian crow	2	Hunt (2000)
<i>Corvus albus</i>	pied crow	2	Goodwin (1986)
<i>Corvus crassirostris</i>	thick-billed raven	2	Goodwin (1986)
<i>Corvus caurinus</i>	northwestern crow	2	Saunders & Ydenberg (1995)
<i>Corvus brachyrhynchos</i>	American crow	2	Cristol (2005)
<i>Corvus ossifragus</i>	fish crow	2	McGowan, personal communication
<i>Corvus cryptoleucos</i>	Chihuahuan raven	2	Goodwin (1986)
<i>Corvus jamaicensis</i>	Jamaican crow	2	Goodwin (1986)
<i>Corvus coronoides</i>	Australian raven	2	Rowley (1973)
<i>Corvus orru</i>	Torresian crow	2	Goodwin (1986)
<i>Corvus ruficollis</i>	brown necked raven	2	König (1920)
<i>Corvus corax</i>	raven	2	Heinrich & Pepper (1998)

However, scrub-jays also cache a number of other food types and, therefore, the number of pine seeds cached is likely to be an underestimate of the total number of items this species caches (Curry *et al.* 2002). In the laboratory, there was no difference between the three species and a fourth species, the Mexican jay (*Aphelocoma ultramarina*, Bednekoff *et al.* 1997) in caching intensity. Therefore, rather than describing caching intensity as a continuous trait, most researchers have used three categories for caching intensity (Healy & Krebs 1992, 1996; Basil *et al.* 1996; Brodin & Lundborg 2003; Lucas *et al.* 2004). We define the three categories as outlined in table 2. In this study, species were categorized as specialized cacher only when there was explicit information available about their caching behaviour being seasonal or when they are dependent on their caches for part of the year. In contrast to previous reports (Healy & Krebs 1992) we classified the Alpine chough (*Pyrrhocorax graculus*) as a

moderate cacher (Strahm 1960; Goodwin 1986). Brodin & Lundborg (2003) deemed the Rook (*Corvus frugilegus*) to be a specialized cacher, however, we classify it as a moderate cacher based on our definition of caching categories.

We used a phylogeny based on a compilation of smaller phylogenies. As the basis for relationships between genera we used the phylogeny by Hope (1989) which is based on morphological characters, while for the within genus affiliations we used various smaller phylogenies (Goodwin 1986; delos Monteros & Cracraft 1997; Cibois & Pasquet 1999; Saunders & Edwards 2000). Branch lengths between genera were set at $3.4\Delta T_{50H}$ and within genera at $1.1\Delta T_{50H}$ (Sibley & Ahlquist 1990; Bennett & Owens 2002).

We used the program MULTISTATE for the evolutionary reconstruction of caching behaviour (Pagel 1997, 1999a,b). MULTISTATE uses a continuous-time Markov model to calculate a maximum likelihood estimate for the phylogenetic

Table 2. Definitions of the three categories of cachers.

specialized	hide large numbers of items of predominantly one type of food and show a seasonal peak in caching intensity, which coincides with availability of that food. Recover their caches often after long intervals and tend to live in areas of high latitude and or altitude with strong seasonal availability of food
moderate	cache throughout the year, they cache a variety of types of food and are never entirely dependent on their caches for survival
non	cache virtually never

model applied. Hypotheses for models of evolution are tested with likelihood ratio statistics. If the likelihood ratio for the two hypotheses is larger than 2, then by convention the hypotheses are considered significantly different (Edwards 1972). Our H_0 assumed that forward and backward transitions are equally likely and a direct transition from specialized cacher to non-cacher, or vice versa, is not possible but always passes through the intermediate state of moderate cacher.

To test the most likely ancestral state for food caching category we fixed the common ancestor of corvids at the three possible states at a time and calculated the likelihood for each. Additionally, we traced where in the phylogeny the major changes in caching category took place by assessing the likelihood for each of the categories at specific nodes within the phylogeny.

3. RESULTS

The literature provided information on caching behaviour for 46 species of corvids from 16 genera (table 1). Six genera consisting of predominantly tropical species are not represented in this study because of a paucity of data.

The model with restricted parameters (H_0) does not show a significantly lower likelihood than a non-restricted model and, therefore, the H_0 is preferred because it is the simpler model (Pagel, MULTISTATE manual). When we left the root free to take any of the three states, the reconstruction suggests that, with a probability of 0.96, the common ancestor of corvids was a moderate cacher. To test whether the state of moderate cacher is significantly preferred over the other states we fixed the root at each of the states and calculated the likelihood for each. When comparing the different states the log likelihood ratio is >2 in favour of the ancestor being a moderate cacher. We conclude, therefore, that the common ancestor of the corvids was most likely a moderate cacher.

The reconstruction of the common ancestor of the New World jay species (node 2, see figure 1) showed that it was a cacher, but there is no significant differentiation between the state of moderate and specialized cacher. Similarly, nodes 6–10 do not show a preference for a reconstruction between moderate and specialized cachers and, therefore, it is not possible to assign either of the two states to the ancestors of three clades (namely the genera *Nucifraga*, *Perisoreus* and *Garrulus*), which are exclusively specialized cachers. However, the common ancestor of the genus *Corvus* is unambiguously reconstructed as a moderate cacher.

These results imply that the transition from moderate cacher to specialized cacher occurred at least twice at nodes 2 and 6, in which case several clades reversed to moderate cachers again. Alternatively, the transition from moderate to specialized cacher took place up to five times,

namely at branches leading to *Gymnorhinus* and *Cyanocitta* and at those leading to *Nucifraga*, *Perisoreus* and *Garrulus*. The state of non-cacher evolved at least twice, once in the clade leading to the white-throated magpie jay (*Calocitta formosa*) and once in the clade leading to the jackdaw (*Corvus monedula*).

4. DISCUSSION

This phylogenetic reconstruction strongly suggests that the common ancestor of the corvids was a moderate cacher. Although many extant corvid species are moderate cachers, there are also some non-cachers and some specialized cachers. Therefore, two opposite evolutionary trajectories to caching behaviour have occurred within the corvids. The first is an evolutionary specialization towards a strong dependence on cached food resulting in highly specialized species and this transition occurred at least twice, and possibly five times independently within the corvids. The second is the loss of caching behaviour and this transition also occurred at least twice independently within the corvids. Below we discuss what the consequences are of these findings for the adaptive specialization hypothesis.

Adaptations underlying efficient cache recovery may be too costly to maintain in those species that lost the propensity to cache. For instance, maintaining an enlarged hippocampus is presumably energetically costly because brain tissue is metabolically expensive (Aiello & Wheeler 1995; Laughlin *et al.* 1998; Attwell & Laughlin 2001). Selection pressures might favour a reduction in the quantity of neural substrate, and thus non-cachers may show reduced hippocampal volumes compared to their caching counterparts. Evidence in support of this claim comes from jackdaws, because these non-cachers have relatively small hippocampal volumes (Healy & Krebs 1992).

Furthermore, adaptations may also be co-opted for other tasks. The hippocampus is involved in other functions than spatial memory alone (Day 2003) and it has been suggested that the hippocampal formation might serve both spatial and episodic memory (Jefferey 2004). Although the western scrub-jay does not have a particularly accurate spatial memory compared to some other corvid species (Balda & Kamil 1989; Kamil *et al.* 1994), it has episodic-like memories of what was cached where and when (Clayton & Dickinson 1998). Perhaps species that cache perishable foods co-opted their hippocampus to encode episodic-like memory, and thus keep track of when items degrade.

The evolution into specialized caching has occurred independently in the clade leading to the Clark's nutcracker and the clade leading to the pinyon jay. Both species have evolved pouches to transport large numbers of seeds to cache locations, however, the pouches differ



Figure 1. Ancestral state reconstruction for caching categories in corvids using maximum likelihood. The squares represent the most likely reconstruction of the caching category at that node. Numbered nodes are referred to in the text. Branch lengths are not proportional to genetic distance.

markedly. Nutcrackers have evolved a sublingual pouch (Bock *et al.* 1973), whereas pinyon jays have evolved an expandable oesophagus (Vander Wall & Balda 1981). In much the same way as the two species have different morphological adaptations, it is conceivable that the increased intensity to cache resulted in an increased capacity to remember the location of large amounts of cached items, but the way this capacity was increased differed between species. We develop this argument on two levels: first, in terms of hippocampal specializations, and second, in terms of memory performance.

Comparative brain studies focus on the volume of the hippocampus as a measure of adaptation (Brodin &

Lundborg 2003 and references therein). Surprisingly the pinyon jay has a relatively small hippocampus (Basil *et al.* 1996), given that it is a specialized cacher. However, there is no inherent reason to focus on volume *per se*. Species could differ in a number of other aspects of hippocampal neuroanatomy such as the number or density of neurons versus glial cells, dendrites per neuron, synaptic connections per neuron (Rogers 2004), as well as in differential rates of recruitment, replacement or survival of new neurons (Barnea & Nottebohm 1994, 1996; Hoshoooley & Sherry 2004). When behavioural specializations are supported by neural adaptations, it need not result in the same neural solutions in species that evolved the

behavioural specialization by convergent evolution (Nishikawa 2002). Thus, the pinyon jay may have evolved a different solution for the increased demand on spatial memory than the Clark's nutcracker.

Similarly, if intense caching evolved independently in two different lineages of corvids, then there is no *a priori* reason to assume that those two lineages have developed the same solution for increased memory performance. Although pinyon jays and nutcrackers have excellent memories for cache locations it is possible that the two differ in the particular solution they use to perform such memory tasks. If evolution has created different solutions for solving the enhanced memory demands of intense food-caching in pinyon jays and nutcrackers, then the two species might show different weaknesses when tested on tasks that tap into different aspects of memory.

Consider two comparative studies of memory performance in corvids. In one study, Clark's nutcrackers (specialized cacher), pinyon jays (specialized cacher), scrub-jays (moderate cacher) and Mexican jays (moderate cacher) were compared on an operant spatial delayed non-matching to sample (DNMTS) task using a touch screen (Olson *et al.* 1995). Although nutcrackers outperformed the other species as expected, surprisingly pinyon jays were no better at this task than the other two jay species. Despite being a specialized cacher like the Clark's nutcracker, the pinyon jay's performance on this task was more similar to its close relatives, the scrub-jays and Mexican jays. Performance on the operant DNMTS task is determined in part by proactive interference from preceding trials. There are two different aspects of memory that may affect proactive interference in spatial DNMTS tasks. One is perseverance, and the second is memory accuracy. Although pinyon jays and nutcrackers show similar perseverance of spatial memory (Bednekoff *et al.* 1997), there may be a species difference in memory accuracy. Pinyon jays tend to cache in clusters, which allows them to use a non-mnemonic strategy for cache recovery, such as area-restricted search, in addition to spatial memory.

Balda & Kamil (1989) allowed pinyon jays and Clark's nutcrackers to cache pine nuts in two conditions, one of which allowed cluster caching and the other did not. As one might predict, pinyon jays were more accurate at recovery of the clustered caches. The surprising result was that the pinyon jays were just as accurate as the nutcrackers in the non-clustered caches condition. However, both species only made eight caches, which is much smaller than observed in the wild and also much smaller than the number of trials in a DNMTS task. Perhaps the pinyon jays would have performed less well if they had been required to cache a lot more items, particularly if they are more susceptible to proactive interference than nutcrackers on cache recovery and on subsequent trials in the DNMTS task. This prediction could be tested directly by comparing the spatial memory accuracy of nutcrackers and pinyon jays when they have cached large numbers of items.

In a second study, Gould-Beierle (2000) compared performance on a radial maze in Clark's nutcrackers, pinyon jays, western scrub-jays and jackdaws. The Clark's nutcracker's performance was no better than that of the non-caching jackdaw, while both were outperformed by the pinyon jay and scrub-jay. As in the previous example,

the species perform more similar to their close relatives than to the species most similar in degree of caching. Perhaps these surprising results can be explained in terms of the species' social structure. Both jay species often encounter cache pilferage by conspecifics, while this is less likely in the more solitary nutcracker. Possibly such pilferage has elicited an evolutionarily arms race resulting in strategies for both pilfering and cache protection (Bugnyar & Kotrschal 2002). For instance, pinyon jays and Mexican jays have excellent spatial observational memory for caches made by other individuals, which is not the case in Clark's nutcracker (Bednekoff & Balda 1996a,b). Nutcrackers often return to earlier inspected sites, which they had found emptied while jays do not return. Perhaps one reason why the pinyon jays and scrub-jays do not revisit earlier inspected cache sites is because they are adapted to cache pilferage.

In conclusion, we showed that the common ancestor of corvids was a cacher. Therefore, it seems likely that all extant corvid species evolved from an ancestor that showed the basic adaptations to caching. Within the corvids some species developed into specialized cachers and these species show even further enhanced adaptations to caching behaviour, such as pouches for transportation. Specialized caching evolved at least twice independently within corvids, and thus the associated adaptations are the result of convergent evolution of behaviour rather than of common descent. Therefore, although the adaptations serve the same functions they may show differences in design and in particular aspects of their performance. We argue that this does not apply only to morphological traits but also to neurological and cognitive traits. When comparing species on neurological and/or cognitive traits, one needs to take their evolutionary history into account.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.